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Changes in the woody component of an East African savanna during 25 years

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ABSTRACT. Changes in density, structure and species composition of the woody component of the two predominant savanna types in Tarangire National Park, northern Tanzania, during a period of 25 y were investigated. The park is known for its large, increasing elephant numbers and high frequency of fires. In 1996 a study on woody species density, composition and age structure, which was first performed in 1971, was repeated, using the same transects and method. Access to the original data of 1971 allowed for a full comparison of the changes and an investigation whether these could be related to changes in elephant numbers and fire frequency. The total tree density declined during the 25 y, but the decline was not evenly distributed over the different height classes. Although the density of trees taller than 5 m declined significantly, the greatest decline occurred in the density of trees shorter than 1 m. The density of trees in the intermediate height class of 1–5 m did not decline. Although damage to trees by elephants increased during the 25-y period, *c.* 25% showed no browse damage and, except for some severely damaged trees, elephant damage was not found to reduce tree vigour. Elephants affected the size distribution of the savanna woody component much more than the density, while the data suggest no significant effect of fire on changes in tree density. The large decline in density of small trees was attributed to a severe drought in 1993. Based on large numbers of elephants during the past decades and on relatively low elephant impact on the total tree density, the present study suggests that the current elephant number of 2300 can be sustained in the park without causing detrimental effects, provided that their current range is maintained.

KEY WORDS: deciduous and microphyll savanna, elephants, savanna structure, Tanzania, tree density, tree species, woodland dynamics

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INTRODUCTION

The vegetation structure of African savannas is in a continuous state of transition, leading to shifting mosaics of woodland and open grasslands (Caughley 1976, Dublin 1995, Sinclair & Arcese 1995). The role that elephants can play in affecting these local transitions has been described by various authors (Ben-Shahar 1993, Buechner & Dawkins 1961, Buss 1990, Caughley 1976, Croze *et al.* 1981, Laws 1970, Sinclair 1995, Van Wijngaarden 1985), many of which associated high elephant densities with a decline in large trees (Abel & Blaikie 1986; Barnes 1983a, b; Caughley 1976, Laws 1970, Lamprey *et al*. 1980, Lewis 1986). Despite the decline in total elephant numbers in sub-Saharan Africa, due to poaching and habitat loss (Douglas-Hamilton 1987, Prins *et al*. 1994), elephant densities have increased in parks and reserves that offer them protection (Barnes 1983b, Douglas-Hamilton 1987). The concurrent loss of large trees caused concern to the managers of these protected areas (Douglas-Hamilton 1972), as large trees provide food and shelter for a variety of animals and are of high aesthetic value (Barnes 1983b, Belsky 1989, Herremans 1995). This concern has become known as 'the elephant problem' (Caughley 1976), and has led to controversial management policies such as culling (Barnes 1983b, Buechner & Dawkins 1961, Laws 1970).

Although many studies emphasized the effect of high densities of elephants on large trees, the question is: can these studies be used to predict long-term changes in the savanna woody component? A decline in large trees does not necessarily lead to a decline in total tree density because large trees are not always killed, but merely reduced in height. In addition, a decline in the density of large trees, for example *Acacia tortilis*, may even enhance the establishment of seedlings which do not grow under the mature canopy (Weyerhaeuser 1982). Consequently the effect of elephants on the savanna woody component may merely result in changes in the age/size distribution of trees rather than a decline in total tree density (Weyerhaeuser 1982). The understanding of the effects of elephants on savanna woodland dynamics is additionally complicated by the fact that the extent to which elephants affect the savanna woody component depends on factors such as tree density, age structure (Barnes 1985), soil type (Van Wijngaarden 1985), other herbivore species (Belsky 1984, Dublin 1995, Pellew 1983, Prins & Van der Jeugd 1993) and fire (Trollope 1996). Both altered herbivore assemblages and increased fire frequency, due to increased human settlement and poaching around protected areas, may consequently also have contributed to savanna woodland change in the past decades.

Therefore, to understand the effect of elephants on savanna woodland dynamics studies on the whole savanna woody component should be performed (Weyerhaeuser 1982), whereby sufficiently long time spans must be considered because these are less sensitive to the short-term oscillations that can provide erroneous indications of long-term trends (Prins & Van der Jeugd 1993). However, data on the long-term effects of elephants on the dynamics of the savanna

woody component are incomplete (Dublin 1995) with no published studies exceeding 20 y with data reflecting long-term changes across all cohorts and tree species.

The aim of this study was to investigate the change in density, structure and species composition of the woody component of the two predominant savanna types in Tarangire National Park, northern Tanzania, during a 25-y period. Tarangire National Park is known for its large herds of elephants and recurrent fires. Many people have stated that the vegetation has become considerably more open in the past decades (Ecosystems Ltd. 1980) and have attributed this to increasing elephant numbers and fire frequency. In 1971, Vesey-FitzGerald (1973b) investigated tree density, structure and composition in two predominant savanna types. The present study repeated this study in 1996, using the same sampling sites and methods. As we had access to the original data from 1971, we were able to analyse changes in the woody component during a 25-y period. The variation in change of tree distribution over different height classes during the 25-y period and spatial variation in elephant density and fire occurrence, allowed for identification of possible causes of the changes observed.

STUDY AREA

Tarangire National Park (N.P.) is situated between latitude 3°40′ and 5°35′S and longitude 35°45′ and 37°E and covers an area of *c.* 2600 km^2. The Tarangire River runs through the park and is one of the main permanent dry season water supplies within the entire 35 000 km^2 Masai Ecosystem (Prins 1987) in which Tarangire N.P. lies. Average rainfall in the park, based on 21 y of data, is 620 mm, which falls primarily from December to May. Two wooded savanna types dominate the park: (1) the microphyll savanna which can be found in the riverine area with dark alluvial, lacustrine soils and has *Acacia tortilis* (Forsk.) Hayne ssp., *Maerua triphylla* A. Rich. var. (Vahl & Gilg), *Grewia* spp. as the dominant tree species; (2) the deciduous savanna situated on the ridges and upper slopes with well-drained red loams of Pre-Cambrian origin and where *Combretum* and *Commiphora* spp. are the dominant trees.

During the past 40 y, elephant numbers in the park have fluctuated markedly. Prior to being gazetted as a protected area in 1958, the Tarangire area was used for wildlife hunting and elephants numbered *c.* 440 (Lamprey 1964). After the park obtained protected status, the elephant population number increased to *c.* 2900 in 1980 (Ecosystems Ltd. 1980). With elephant population estimates of 440 in 1960 and 2900 in 1980 in Tarangire National Park, the annual increase in elephant numbers during this period, resulting from increase through birth and immigration, would be 9%. Using this annual growth rate, we can estimate that in 1971 there were 1200 elephants. At the end of the 1970s heavy poaching started in and around the park and elephant numbers plummeted (Ecosystems Ltd. 1980). After the mid-1980s, poaching pressure was reduced and the number of elephants started to increase again,

reaching 2300 by 1996 (TCP 1995). Elephant numbers also increased owing to movement of elephants into the park from other, non-protected, areas where human settlement and commercial farming have increased drastically in the past 20-y period (Borner 1985, TWCM 1994).

The majority of the elephants using the park disperse during the wet season into surrounding areas to forage. In the dry season they return to the park because the Tarangire River is their major water source in the dry season. During the dry months, elephants switch from predominantly grazing to predominantly browsing (Beekman & Prins 1989, Buss 1990, Sinclair 1995, Western & Lindsay 1984), and it is during this period that the impact on woody vegetation is likely to be highest (Barnes 1982, Laws 1970).

The frequency of fires also increased in the past decades in Tarangire N.P. The park experiences regular dry season fires, most of which are of anthropogenic origin from outside the park, even though park managers adopted an early dry season burning policy between 1984 and 1994 to counter these fires.

METHODS

This study replicated the transects and methods used by Vesey-FitzGerald in 1971 (Vesey-FitzGerald 1973b: Figure 1). He drew the original transect locations on a park map (1 : 100 000) and on the original data sheets he provided detailed information on the starting point of the transects through various roads and landmarks and compass bearing of transect directions. This allowed us to relocate and repeat the transects accurately and we estimate that the error of the transect starting point is no more than ±200 m. Twenty transects were located in the microphyll savanna and 12 in the deciduous savanna. These two vegetation types were originally chosen because they were the most dominant vegetation types and provided the bulk of browse material (Vesey-FitzGerald 1973b).

The point-centred quarter method (PCQ, Cottam & Curtis 1956) was used to determine tree density. This method was selected by Vesey-FitzGerald (1973b) because it is suitable for determining the density of sparsely spaced trees (Mueller-Dombois & Ellenberg 1974), such as those in savanna systems. PCQ is a plotless sampling technique in which a number of sampling points are selected along a transect of fixed direction. A total of 50 points were sampled per transect with 25-m intervals between consecutive points. Thus each transect covered a distance of 1250 m. At each sampling point, the perpendicular to the transect direction was used to obtain four quadrants. In each quadrant, the distance (d) from the centre point to the nearest woody plant, taller than 50 cm, was measured in m. We did not record trees shorter than 50 cm because this was not done during the original study, most likely because they are too easily overlooked in the grass. A total of 200 trees were sampled per transect and no individual tree was measured twice. A total of 6400 trees

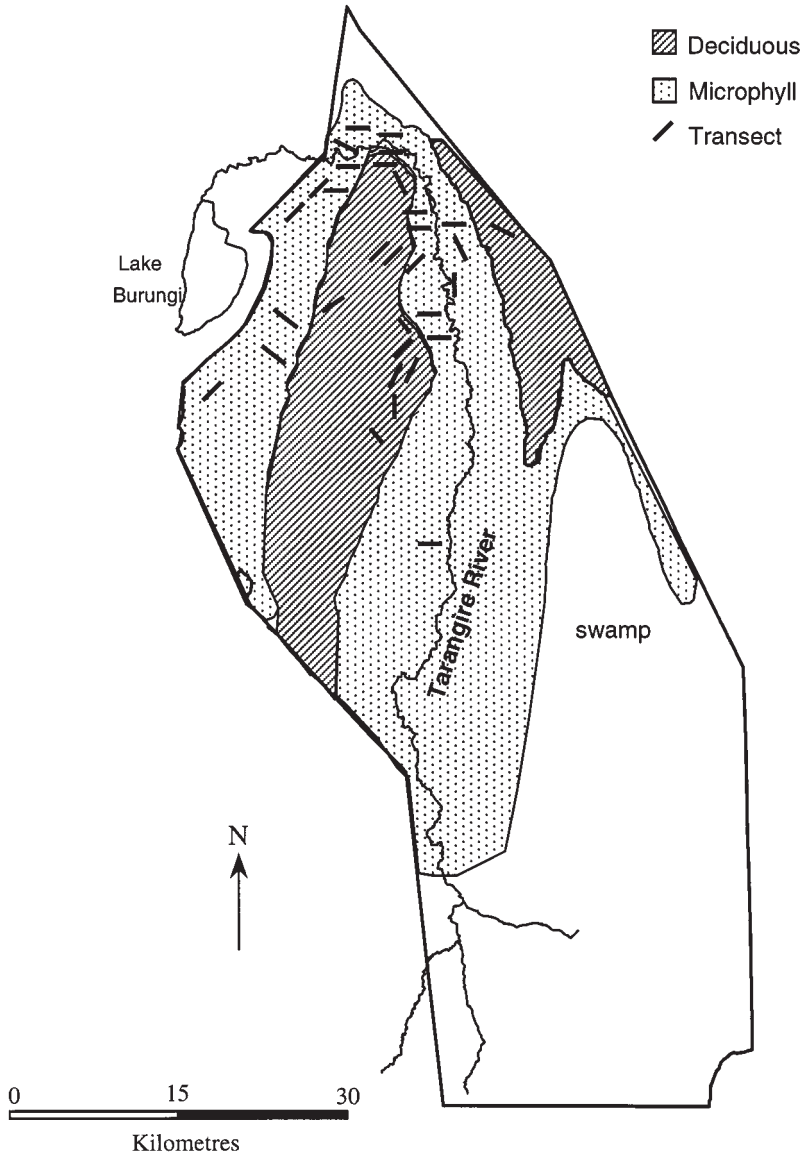

Figure 1. Map of Tarangire National Park showing transect locations and vegetation types in 1996.

were recorded along the 32 transects. The number of trees per hectare (D) was calculated for each transect as:

$$D = \frac{10\,000}{(\bar{d})^2}$$

where $\bar{d}$ = the mean d of a transect (m).

Species, diameter at base, height and crown radius were also recorded for

each tree. Crown area was calculated using the estimated average radius of the tree canopy. Multiplication of crown area with density estimates was used to determine woody cover. Tree height was classified according to vegetation stratum as done by Vesey-FitzGerald (1973b). Trees > 0.5 and ≤ 1 m were distinguished as a separate group because these are still within the herbaceous layer, where they still have to compete for light with the herbaceous vegetation and are extremely susceptible to fire damage (Trollope 1996). Trees > 1 and ≤ 5 m tall were classed separately because they include the majority of shrubs. Trees > 5 m and the canopy height of ≤ 10 m were classed separately from those in the canopy level (>10 m) which were distinguished as fully grown. For the nine most frequently occurring species in the two savanna types, data were also analysed at the species level.

Trees were further classified by browser damage and condition scales, each having four levels. The four damage levels, based on the criteria used by Vesey-FitzGerald, were: (1) no damage – no damage or slight evidence of browsing on leaves; (2) light damage – twigs and small branches lightly damaged; (3) heavy damage – damage to trunk, branches or stem, branches broken and bark ripped off with the structure of the tree significantly altered; (4) extensive damage; tree trunk severely damaged, multiple branches broken, leaves denuded. Condition scores were as follows: (A) good – perfect condition and vigorous growth; (B) average – tree healthy but leaf cover not complete and not all leaves in good condition; (C) poor – leaf growth uneven and leaves in poor shape, dead branches clearly present; (D) very poor – tree dying and leaves, if present, in bad condition, majority of branches dead.

Within the two savanna types, the occurrence of elephants and fires were not evenly distributed. Hence we were able to group transects into 'high' and 'low' elephant occurrence transects, and 'high' and 'low' fire frequency transects. Distinction of 'high' and 'low' elephant presence was based on 4 y of observation (1993–1996) by the second author. The 'high' and 'low' elephant occurrence concurred with the occurrence of other herbivores. Therefore, the transects were categorized as 'high' and 'low' herbivore occurrence areas whereby we assume that these relative densities did not change in the park during the 25-y period. Distinctions between 'high' and 'low' fire frequencies areas were based on fire mapping during the period 1990–1996. Transects in areas that had burned in this period were categorized as having a 'high' fire occurrence, while those that had not burned were categorized as having a 'low' fire occurrence. No transect with a 'high' fire occurrence burned more than once during the 6-y period.

Statistical analysis

Because we had access to the original data of Vesey-FitzGerald (1973b), we were able to do a full comparison of the data collected in 1996 with those of 1971. Prior to statistical analysis, all density estimates were log-transformed to meet the requirements of parametric analysis.

Changes in tree density during the 25-y period were assessed using general linear model analysis (GLM) with the two years and four height classes as fixed effects and transect as a random effect. The analysis was run separately for each savanna type because the two savanna types had unequal numbers of transects and therefore savanna type could not be put into the model. To test whether any changes in density varied between savanna type, differences in density between 1971 and 1996 were tested in a Student's t-test. Student's t-test was also used to analyse the differences in density between the two savanna types. Change in density of individual height classes and species over the 25-y period was tested 'a posteriori', using a paired t-test with tree density as dependent and individual transects in 1971 and 1996 as pairs. Change in the relative frequency, damage levels and canopy area between 1971 and 1996 for individual height classes and species were tested with Wilcoxon's matched pairs test because distributions could not be normalized, due to too many zeros.

Additionally, linear regression analysis was used to investigate whether variation in density change during the 25-y period could be explained by fire occurrence, herbivore occurrence or savanna type. Difference in density between 1971 and 1996 was entered as the dependent variable. Fire occurrence, relative herbivore density and savanna type, with all interactions, were entered as factors using a stepwise procedure.

RESULTS

In 1972 and 1996, tree density was significantly higher in the deciduous savanna than in the microphyll savanna ($t = 167$, $df = 19$, $P < 0.001$ and $t = 15.56$, $df = 11$, $P < 0.001$ for 1971 and 1996 respectively) and tree density declined with increasing height class (Tables 1 and 2a). During the 25-y period, tree density declined in both savanna types, but the decline did not differ between savanna types ($t = 0.133$, $df = 30$, $P > 0.05$). The decline in density did however differ between height classes (Table 2a).

The major part of the decline in tree density was caused by a decline in the

Table 1. Average tree density (ha^{-1}) of height classes and all trees (total) in the microphyll and deciduous savanna in Tarangire National Park in 1971 and 1996. Change (%) gives the difference in density between years as a percentage of the 1971 density. Negative percentage indicates a decline. Asterixes indicate a significant change in density as measured by a paired t-test.

	Microphyll savanna			Deciduous savanna		
Height class (m)	1971	1996	Change (%)	1971	1996	Change (%)
0.5 – ≤1	473	262	–45***	978	513	–48**
1< – ≤5	139	142	2	252	426	69
5< – ≤10	6	4	–33	47	12	–74***
>10	12	3	–75**	2	1	–50
Total	630	411	–35**	1279	952	–26

*, P, $P \leq 0.05$, **, $P \leq 0.01$, ***, $P \leq 0.001$.

Table 2. Variance ratios from an ANOVA (repeated measurements; GLM) of tree density with (a) year (1971, 1996) and height class (0.5–1, 1–5, 5–10 and >10 m) as fixed factors and transect as random factor, and (b) year (1971, 1996) and the nine most common species as fixed factors and transect as random factor.

	Source	Microphyll savanna	Deciduous savanna
(a) Height classes			
	Year (Y)	10.62**	26.59***
	Height class (HC)	270.1***	202.6***
	Transect (T)	1.42	3.97*
	Y× HC	2.07*	6.61***
	Y× T	1.04	0.61
	HC× T	1.12	2.07*
(b) Species			
	Year (Y)	4.55*	3.42
	Species (S)	15.00***	32.87***
	Transect (T)	1.04	1.36
	Y× S	6.07***	7.46***
	Y× T	0.97	0.93
	S× T	3.14***	2.29***

*, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

0.5–1 m height class in both savanna types (Table 1). Excluding this height class from the analysis resulted in no significant changes between 1971 and 1996 ($t = 0.83$, $df = 20$, $P > 0.05$ and $t = 0.507$, $df = 10$, $P > 0.05$ for the microphyll and deciduous savanna respectively). In the microphyll savanna the density of large trees (>10 m) declined by 75%, while no significant decline was found for the 1–5 and 5–10 m height classes (Table 1). In the deciduous savanna, the density of the 5–10 m height class declined by 74% while the density of large trees (>10 m) declined, but not significantly, from 2 to 1 tree per hectare (Table 1). In contrast, the density of trees in the 1–5 m height class increased by 69%, although this was not significant.

A change in the height frequency distribution in the microphyll and deciduous savanna occurred during the 25-y period, with an apparent decline in the frequency of trees between 0.5 and 1 m and an increase of trees between 1 and 5 m (Table 3). Additionally, the low frequency of trees above 10 m in the microphyll savanna dropped significantly, while in the deciduous savanna the frequency of trees in the 5–10 m height class declined (Table 3).

Table 3. Frequency of height classes, expressed as percentages, in the microphyll and deciduous savanna in 1971 and 1996. Asterixes in the 1996 column indicate significant change in frequency between 1971 and 1996 as measured by a Wilcoxon's matched pairs test.

	Microphyll savanna		Deciduous savanna	
Height class (m)	1971 (%)	1996 (%)	1971 (%)	1996 (%)
0.5–≤1	75.0	63.7*	76.4	53.8**
1<–≤5	22.0	34.5*	19.7	44.7**
5<–≤10	1.0	1.0	3.7	1.3**
>10	1.9	0.7**	0.2	0.2*

*, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

Change in density during the 25-y period varied significantly between species, with a decline in *Balanites aegyptiaca* (L.) Del., *Maerua triphylla*, *Commiphora* and *Combretum* spp. and an increase in *Cordia* spp. and *Acacia tortilis* (Table 2b, Table 4). For the other species listed (Table 4), no significant changes were found. Decline in density of specific species was primarily the result of a decline in the 0.5–1 m height class while increase in density was the result of an increase in the 1–5 m height class (Table 4). Finally, of all trees listed, only *Acacia tortilis* and *Balanites aegyptiaca* still had trees in the large phase, although their density had declined significantly since 1971 (Table 4).

Stepwise regression procedure revealed that variance in the decline of total tree density could be explained only by the relative herbivore occurrence ($r^2 = 0.26$, $F = -3.23$, $P < 0.01$), with a greater decline in the high occurrence areas. The same analysis, with the individual height classes investigated as dependent, revealed that only for the 1–5 m height class the herbivore occurrence significantly contributed to the variance in decline ($r^2 = 0.34$, $F = -4.09$, $P < 0.001$). For total density and the separate height classes, the other two factors, fire occurrence and savanna type, as well as the various interactions, did not contribute significantly to the model. However, the low r^2-value does show that most of the variance was not explained by the model.

Tree cover declined during the 25-y period, but the decline depended on savanna type and height class. Figure 2 demonstrates that in the microphyll savanna the decline in cover from 24.7% in 1971 to 10.3% in 1996 ($z = -3.35$, $P < 0.001$) was caused by the >10 m height class which declined from 18 to 4% ($z = -3.46$, $P < 0.001$) while no significant changes occurred in the lower height classes. In the deciduous savanna decline in tree cover was only 5% ($z = -2.05$, $P < 0.05$). This less acute decline was due to a significant increase in the cover of the 1–5 m height class ($z = -2.05$, $P < 0.05$), even though the cover of the 0.5–1 m and 5–10 m height classes declined ($z = -2.85$, $P < 0.01$ and $z = -2.93$, $P < 0.01$ respectively)

Damage level to trees increased during the 25-y period in both savanna types, but the increase differed between height class and species (Figures 3 and 4; Table 5). The major shift was from trees with 'no damage' to trees with 'light damage' (Figure 3). The frequency of trees with 'extensive damage' also increased, especially in the 0.5–1 m height class. But, despite the increase, the frequency of 'extensively damaged' trees remained low. The frequency of trees with 'heavy damage' in the deciduous savanna also increased. Except for the 5–10 m height class, we also found significant correlations (Spearman's coefficient for rank) between the damage levels to trees and the diameter at base for the 0.5–1 m, 1–5 m and >10 m height classes. The average diameter at base ranged from 1.6 cm for trees with 'no damage' to 5.9 cm for trees with 'extensive damage' for the 0.5–1 m height class ($r_s = 0.376$, $P \leq 0.01$), 4.9 to 11.7 cm for the 1–5 m height class ($r_s = 0.313$, $P \leq 0.01$) and 53.6 to 79.2 cm for trees taller than 10 m ($r_s = 0.431$, $P \leq 0.01$). The most obvious difference

Table 4. Average tree density (ha^{-1}) for different height classes and totals of the nine most common species and genera in the microphyll and deciduous savanna. Asterixes indicate significant changes in density as measured by the paired t-test.

Species	Height class (m)	Microphyll savanna			Deciduous savanna		
		1971	1996	P	1971	1996	P
Acacia tortilis	0.5 – ≤1	67.5	71.7	–	1.4	9.9	**
	1< – ≤5	9.7	21.1	**	0.4	2.3	–
	5< – ≤10	0.6	1.1	–	0	0	
	>10	8.5	2.7	*	0	0	–
	Total	86.3	96.6	–	1.8	12.2	**
Balanites aegyptiaca	0.5 – ≤1	17.9	4.1	***	1.6	0.9	–
	1< – ≤5	3.2	2.0	–	5.7	0	–
	5< – ≤10	0.9	1.2	–	0.6	0	–
	>10	2.7	0.1	**	0	0	
	Total	24.7	7.4	***	7.9	0.9	–
Maerua triphylla	0.5 – ≤1	56.7	23.5	**	0.7	1.3	–
	1< – ≤5	29.1	31.7	–	0	0.5	–
	5< – ≤10	0	0	–	0.7	0	–
	>10	0	0	–	0	0	–
	Total	85.8	55.2	**	1.4	1.8	–
Dalbergia melanoxylon	0.5 – ≤1	21.5	12.8	–	82.8	77.5	–
	1< – ≤5	12.1	6.1	–	24.6	35.5	*
	5< – ≤10	0.7	0.3	–	0.6	1.4	–
	>10	0	0	–	0	0	–
	Total	34.3	19.2	–	108.0	114.4	–
Commiphora spp.	0.5 – ≤1	51.2	8.6	***	241.6	61.8	***
	1< – ≤5	5.0	7.9	–	22.5	16.3	*
	5< – ≤10	0.4	0	–	1.8	0	–
	>10	0.1	0	–	0	0	–
	Total	56.7	16.6	***	265.9	78.1	***
Combretum spp.	0.5 – ≤1	9.0	0.7	**	278.2	138.0	–
	1< – ≤5	3.8	0.6	–	101.0	226.7	**
	5< – ≤10	0.1	0	–	35.0	9.4	***
	>10	0	0	–	0.2	0	–
	Total	12.9	1.3	*	414.4	374.1	–
Grewia spp.	0.5 – ≤1	107.9	73.8	–	52.6	60.6	–
	1< – ≤5	34.8	15.9	–	39.4	44.8	–
	5< – ≤10	0	0.1	–	0.4	0.2	–
	>10	0	0	–	0	0	–
	Total	142.7	89.8	–	92.4	105.6	–
Markhamia spp.	0.5 – ≤1	36.4	18.6	–	24.3	7.1	–
	1< – ≤5	10.3	17.7	–	7.4	18.5	–
	5< – ≤10	0	0	–	0	0.7	–
	>10	0	0	–	0	0	–
	Total	46.7	36.3	–	31.7	26.3	–
Cordia spp.	0.5 – ≤1	6.2	10.1	–	1.0	7.2	**
	1< – ≤5	9.7	17.1	**	2.3	11.1	**
	5< – ≤10	0.3	0.1	–	0	0.1	–
	>10	0	0	–	0	0	–
	Total	16.2	27.3	**	3.3	18.4	**

–, $P > 0.05$; *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

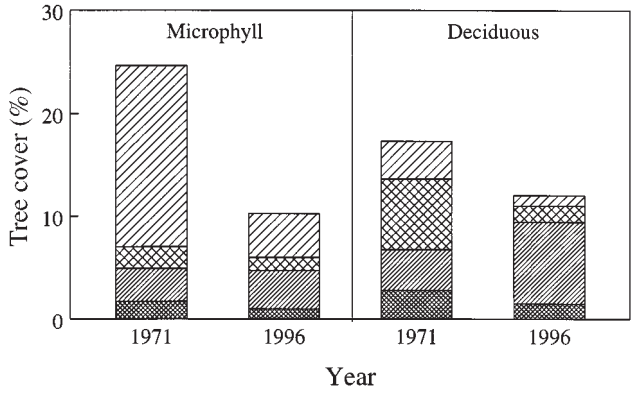

Figure 2. Cover of woody vegetation as a percentage of total area for the different height classes in the microphyll and deciduous savanna in 1971 and 1996. ▩, 0.5 – ≤1 m; ▨, 1 < – ≤5 m; ▩, 5 < – 10; ▨, > 10 m.

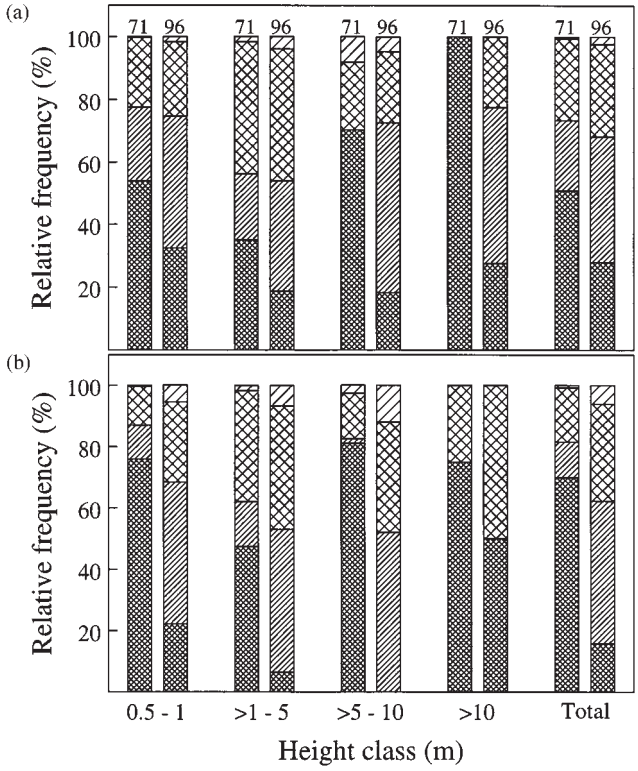

Figure 3. Relative frequency of damage class (▩, no damage; ▨, light damage; ▩, heavy damage and ▨, extensive damage) for the different height classes and all trees (Total) in (a) the microphyll savanna, and (b) deciduous savanna, in 1971 (71) and 1996 (96).

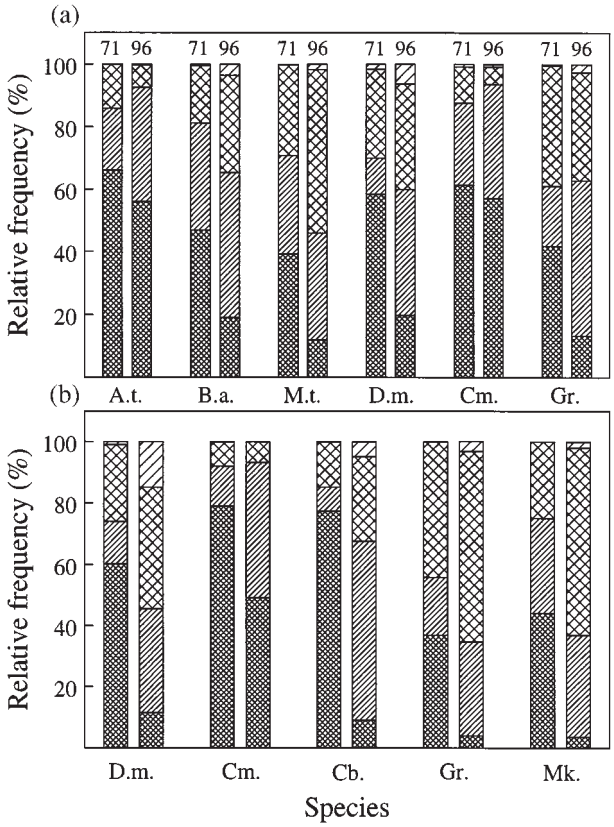

Figure 4. Relative frequency of damage class (▩, no damage; ▨, light damage; ▩, heavy damage; and ▨, extensive damage) for the predominant tree species and genera in (a) the microphyll savanna and (b) deciduous savanna in 1971 (71) and 1996 (96). A.t., *Acacia tortilis*; B.a., *Balanites aegyptiaca*; M.t., *Maerua triphylla*; D.m., *Dalbergia Melanoxylon*; Cm., *Commiphora* spp.; Cb., *Combretum* spp.; Gr., *Grewia* spp.; M.k., *Markhamia* spp.

in the damage level between individual species was the relatively large increase in damage for *Dalbergia melanoxylon* Guill. & Per. which contrasted with the relatively small increase for *Commiphora* spp. (Figure 4, Table 5).

No data on tree condition in 1971 were available. Tree condition in 1996 was better in the microphyll than the deciduous savanna ($\chi^2 = 17.49$, df = 3, $P < 0.001$) (Figure 5a, b). The main cause of this difference was a higher frequency of trees in the average condition class in the microphyll savanna ($\chi^2 = 23.71$, df = 1, $P < 0.001$). The majority of trees were in good to average condition with little difference between height classes, although the condition of large trees tended to be slightly higher. Very few trees were in a very poor condition and dying, 1% and 0.6% for the microphyll and deciduous savanna respectively. Larger differences were found in condition between tree species (microphyll: $\chi^2 = 361.3$, df = 6, $P < 0.001$; deciduous: ($\chi^2 = 144.9$, df = 6, $P < 0.001$). *Acacia tortilis* and *Commiphora* spp. were in better than average condition while *Grewia* spp. and *Markhamia* spp. were in poor condition (Figure 5c, d).

Table 5. Z-values of Wilcoxon paired comparisons (with transects in 1971 and 1996 as the pairs) of damage levels in the microphyll and deciduous savanna for different height classes and all trees (total) and for the predominant woody species.

Height class (m)	None	Light	Heavy	Extensive
Microphyll savanna				
0.5 – ≤1	–3.54***	–3.22**	–1.81	–3.17**
1< – ≤5	–2.41*	–3.06**	–2.42	–1.76
5< – ≤10	–2.52*	–2.67**	–0.40	–1.00
>10	–2.80**	–2.67**	–2.02*	–
Total	–3.58***	–3.42***	–1.73	–2.60**
Species				
Acacia tortilis	–3.57***	–3.29***	–0.36	–0.26
Balanites aegyptiaca	–2.78**	–2.04*	–0.59	–1.34
Maerua triphylla	–3.14**	–2.54**	–1.30	–1.82
Dalbergia melanoxylon	–2.02*	–2.2*	–1.01	–1.21
Commiphora spp.	–0.80	–0.86	–2.13*	–1.00
Grewia spp.	–3.07**	–3.07**	–1.32	–1.33
Deciduous savanna				
0.5 – ≤1	–2.81**	–2.80**	–2.20*	–2.29*
1< – ≤5	–2.80**	–1.99*	–0.97	–1.84
5< – ≤10	–2.20*	–0.81	–0.94	–1.07
>10	–	–	–	–
Total	–2.80**	–2.80**	–2.29*	–2.19*
Species				
Dalbergia melanoxylon	–2.24*	–1.26	–1.82*	–0.94
Commiphora spp.	–2.70**	–0.96	–0.41	–1.00
Combretum spp.	–2.80**	–2.59**	–0.51	–2.20*
Grewia spp.	–2.07*	–1.54	–0.53	–2.02*
Markhamia spp.	–1.09	–0.37	0	–1.00

–, P > 0.05*; P, P ≤ 0.05; **, P ≤ 0.01; ***, ≤ 0.001.

DISCUSSION

Various reports mention that increasing elephant numbers and re-occurring fires were having a major impact on the woody component of Tarangire N.P. (Ecosystems Ltd. 1980). H. Lamprey (*pers. comm.* 1991) and I. Douglas-Hamilton (*pers. comm.* 1993) estimated that more than 50% of the large trees in the Tarangire valley had disappeared since the 1960s. This period was one during which the number of elephants reached 2900 in 1980, then plummeted, but then increased to 2300 in 1996, a number double the previously estimated 1200 of 1971. These reports on woodland change in Tarangire were however all based on circumstantial evidence. Since we replicated the research performed by Vesey-FitzGerald (1973b), using the same transects and including all trees above 0.5 m, the changes in the whole savanna woody component during a period of 25 y could be investigated.

Present data show that during the 25-y period the tree density declined and changes occurred in the structure and species dominance in both savanna types investigated in Tarangire N. P. The total tree density in the microphyll and deciduous savannas declined by 35 and 26% respectively, which could be

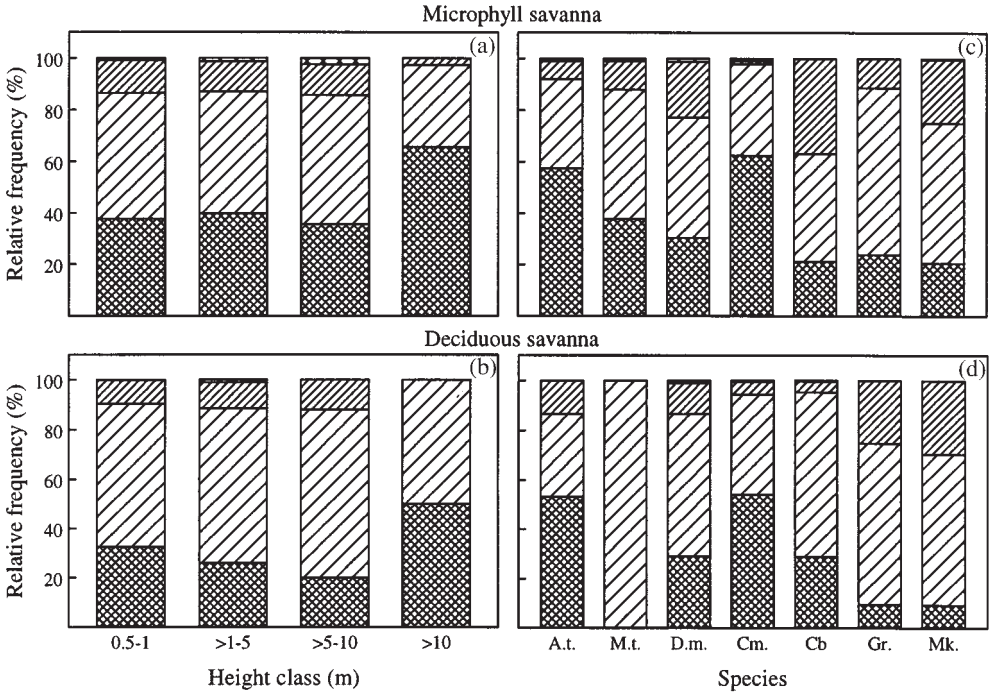

Figure 5. Relative frequency of tree condition in 1996 in the microphyll and deciduous savanna in different height classes (a,b) and species and genera (c,d). ▩, perfect condition and vigorous growth; ▨, average condition, tree healthy but leaf cover not complete and not all leaves in good condition; ▨, poor condition, leaf growth uneven and leaves in poor shape, dead branches clearly present; ▩, very poor condition, tree dying – leaves, if present, in bad condition, majority of branches dead. A.t., *Acacia tortilis*; M.t., *Maerua triphylla*; D.m., *Dalbergia Melanoxylon*; Cm., *Commiphora* spp.; Cb., *Combretum* spp.; Gr., *Grewia* spp.; M.k., *Markhamia* spp.

expected to reflect the increase in elephant density and fire occurrence. However, the decline was not evenly distributed over the different height classes identified. The most apparent decline occurred in the 0.5–1 m height class which, when excluded from the analysis, resulted in no significant decline in tree density during the 25-y period. Conversely, the density of trees in the intermediate height class of 1–5 m did not decline and even tended to show an increase in the deciduous savanna while the already low density of large trees taller than 5 m in 1971, declined even further.

Changes in tree density and structure did not differ between savanna types, but the cover of woody species did decline more in the microphyll than the deciduous savanna. This difference in decline can be attributed to a strong decline in the cover of large trees in the microphyll savanna, while the cover of trees in the 1–5 m height class in the deciduous savanna increased. The presented difference in change between tree density and cover demonstrates that savanna woodland dynamics are not accurately reflected by the woody cover alone and indicates that erroneous conclusions can be drawn when aerial

observations of tree canopy are used to determine the effect of elephants on the savanna woody component.

Because the effects of elephants and fire on the savanna woody component vary with tree size, and because elephant density and fire occurrence varied between transects, the present study allows for a discussion of the possible causes for the observed changes in the density of the identified height classes and species frequency.

Large trees

The large decline in trees taller than 5 m concurs with the estimates of H. Lamprey (*pers. comm.* 1991) and I. Douglas-Hamilton (*pers. comm.* 1993). This decline as well as the observed increase in damage levels to large trees probably reflects the increase in elephant impact on large trees during the 25-y period.

However, it can be questioned whether this decline is due to mortality of large trees and whether elephants are the prime cause of this mortality. Although the increased damage levels, as compared to 1971, reflect high elephant usage of large trees, we only found a small percentage of large trees with extensive elephant damage and none of these trees appeared to be dying as a result of current elephant usage. We did, however, find stands of large *Acacia tortilis*, the predominant large tree in the Park, that had died but showed no signs of elephant damage. This suggests that increased mortality of large trees may be partly due to causes other than elephants such as change in ground water tables (Weyerhaeuser 1982) and life-state dependent processes since many of the large *Acacia tortilis* in East African savannas are from a single cohort. These trees became established at the turn of the century when rinderpest first struck sub-Saharan Africa (Prins & Van der Jeugd 1993). Herbivore density and fire frequency declined dramatically which led to bush encroachment in many parts of East Africa (Dublin 1995). These trees may now be reaching maximum age, and hence have started to die (Western & Van Praet 1973, Young & Lindsay 1988).

It can also be questioned whether the decline in large trees is due to mortality or whether elephants merely browsed large trees down to smaller size classes. Much elephant usage of big trees is through the breaking of branches, which does not necessarily kill trees but converts them to smaller height classes (Buss 1990, Pellew 1983).

Intermediate sized trees

Our data show that, in contrast to the other height classes, the 1–5 m height class did not decline in the microphyll savanna, and even tended to increase in the deciduous savanna. Increased damage levels in the 1–5 m height class during the 25-y period reflect the high use by elephants of this height class. Damaged trees in this height class had greater base diameters than undamaged trees. This indicates that they were either formerly taller trees that have

been knocked down to a lower height class by elephants, or have been prevented from growing into the next height class by repeated elephant feeding or browsing by other browsers. The significant relationship between change in tree density and relative herbivore occurrence would additionally suggest high elephant browsing on this height class. All these findings correspond well with other studies that have shown that the preferred feeding height for elephants is within the 1–5 m range (Barnes 1983a, Buss 1990, Croze 1974, Jachmann & Bell 1985).

Despite the increase in damage to trees in the 1–5 m height class, the majority were in average to good condition and many damaged trees had responded by coppicing. This has also been noted in other studies (Caughley 1976, Guy 1981, Jachmann & Bell 1985, Lawton & Gough 1970, Lewis 1991). In Tarangire several woody species, notably *Combretum* spp., *Dalbergia melanoxylon*, *Maerua* spp., *Grewia* spp., and *Acacia tortilis*, responded to elephant damage by coppicing. Although these species showed higher damage levels than in 1971, their condition was average to good, and their densities either remained stable or increased, as was the case for *Acacia tortilis* in the microphyll savanna and *Dalbergia melanoxylon* and *Combretum* spp. in the deciduous savanna (Table 4). This indicates that a change in species abundance due to elephant browsing may not only be the result of preferential selection by elephants (Field 1971, Guy 1981, Jachmann & Croes 1991, Lewis 1991, Vesey-FitzGerald 1973a), but also the result of the differing ability of tree species to respond to damage by coppicing (see also Barnes 1983a).

Small trees

At first glance the strong decline in density and increased damage levels of the 0.5–1 m height class would suggest a significant impact of elephants on this height class. However, there is conflicting evidence as to whether elephants have much impact on trees less than 1 m tall. Some studies found that elephants omit this size category by disproportionately feeding on woody species taller than 1 m (Croze 1974, Jachmann & Bell 1985, Norton-Griffiths 1979, Pellew 1983, Vesey-FitzGerald 1973a). However, when this browse becomes less abundant, elephants divert browsing to small trees and can become a major factor in mortality of trees smaller than 1 m (Dublin 1995).

Pellew (1980) found a high positive relation between tree cover and available browse. Hence, the high cover percentage of trees in height classes above 1 m in Tarangire N.P. would suggest that the majority of browse was present above 1 m. This would suggest that elephant feeding would not have concentrated on the 0.5–1 m height class. However, we also found an increase in damage to small trees. At the same time we found damage and diameter at base to be correlated with some extensively damaged trees having basal diameters of 18 cm. This suggests that increased damage level to trees in this height class is not so much the result of increased elephant damage to the small trees but rather is the result of elephants browsing larger trees down to this height class.

Besides elephants, ample evidence exists that other browsing animals affect density of small trees (Croze 1974, Belsky 1984, Dublin *et al*. 1990, Prins & Van der Jeugd 1993). We also found, however, that the decline in density of trees in the 0.5–1 m height class was not greater in areas where the occurrence of herbivores is high.

Fire is another factor that is known to have a large impact on small trees (Trollope 1984), but only under severe, annual burning will the density of small trees be reduced (Dublin 1995). This may explain why we found no significant difference in decline in tree density between the 'high' and 'low' fire frequency areas. No transects in the 'high' fire frequency areas experienced two consecutive severe fires in the 1990–1996 period, the period that fire occurrence was monitored.

Finally, density of small trees can be very much dependent on rainfall since this has a strong impact on germination rates and seedling establishment (Gerhardt 1993). In 1993 a severe drought afflicted Tarangire with only 50% of the average rainfall falling. It might therefore well be that the significant lower density of the 0.5–1 m height class in 1996, as compared to 1971, is due to the drought in 1993.

Final suggestions

Why did the increased elephant numbers in Tarangire National Park not result in a large decline in tree density as has been described in other studies (Abel & Blaikie 1986; Barnes 1983a, b; Caughley 1976, Laws 1970, Lamprey *et al*. 1980, Lewis 1986)? We suggest that this can be explained in the following way.

The annual increase of elephant numbers in the park of 9% between 1960 and 1980, due to birth and immigration, is high, reaching maximum elephant population growth rates (Calef 1988; H. H. T. Prins & C. Moss, *pers. comm.*). This suggests that elephants were not limited by forage supply during this period. Furthermore, elephants congregate in the park during the dry season, when their diet is predominantly browse (Buss 1990, Dublin 1995, Western & Lindsay 1984). These observations would suggest that the supply of dry season forage in Tarangire N.P. does not seem to be limiting when elephant numbers are below *c*. 3000, as is currently the case. We did not investigate the annual production of browse in Tarangire. However, in other studies highly significant correlations were found ($r < 0.95$) between browse production and tree diameter (Cissé 1980, Pellew 1980, Rutherford 1978). Using these browse production estimates browse production in Tarangire would range between 350 to 1000 kg ha^{-1} y^{-1}. Given the current elephant numbers of *c*. 2300, average elephant mass of 1800 kg and elephant daily forage intake (dry weight) of 2% live body mass, maximum annual browse would be *c*. 116 kg ha^{-1} y^{-1}. This shows that annual browse production more than compensates for annual elephant browse, even if the conservative estimate of 350 kg ha^{-1} y^{-1} were to be considered. The average of 25% trees that had no browse damage does indeed suggest that browse production exceeds the annual browse consumption in the park.

Furthermore, elephants move to foraging areas outside the park during the wet season, allowing trees to recover from dry season browsing through coppicing. If access to foraging areas outside the park were to be blocked and the elephant population growth were to remain high, elephant usage may reach levels at which response by coppicing of trees would decline. This might consequently result in the more dramatic decline in tree density as experienced in other parks where elephant densities were as high as 6 km^{-2} (Prins & Douglas-Hamilton 1989).

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